THE XEROPHYTIC STRUCTURE OF THE LEAF IN THE AUSTRALIAN PROTEACEAE. Part i.

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(Plates xxiii-xxv and 27 Text-figures.)

[Read 31st August, 1927.]

The endemic Angiosperm flora of Australia is, for the most part, strongly xerophytic, and this characteristic reaches its highest development in the Proteaceae, every species, even those growing in the coastal rain-forests, showing xerophytic adaptations in some degree, the genera *Isopogon*, *Petrophila*, *Grevillea*, *Hakea*, *Banksia* and *Dryandra* being highly specialized in this direction.

Most of the recognized devices for checking transpiration are found in the plants of this family—alteration of the orientation of the leaf, reduction of leaf surface, thickening and cutinization of the epidermis, occurrence of hypoderm, sunken stomates, palisade cells in two rows and closely packed, reduction of intercellular spaces, larger water-carrying vessels than in mesophytes, an enormous development of sclerenchyma and the presence of tannin in considerable quantities. In some species the leaf margin is recurved so as to form, with the midrib, two parallel grooves, which are lined with hairs. The stomates are placed in these grooves, and the hairs not only protect against heat, but check transpiration by surrounding the stomates with a still atmosphere saturated with water vapour. In another group of species the stomates are placed in balloon-shaped cavities on the underside of the leaf; these cavities are lined with hairs, the filiform extremities of which form a plug to the orifice, thus preventing the free interchange of air.

Reduction of leaf-surface is very common, but it is not carried to the extreme of actual leaflessness as it is in many other families. Most species have a coating of two-armed hairs in the juvenile stage of the leaf, but as a rule the arms drop off as the leaf develops, leaving the base embedded in the thickening epidermis. But no species has a dense coating of hair persisting throughout the life of the plant as in the South African *Leucadendron*. *Adenanthos cygnorum* is the only Australian Protead I know which has a permanent coating of hair, and it is much thinner and woollier than *Leucadendron*. Some of the Grevilleas have a dense coat of hair on the underside of the leaf, which is persistent.

Most of the species have several of these adaptations in their leaves. Coatings of bloom, wax, varnish or hygroscopic salts are absent, so far as I know, in the Australian Proteaceae, and ethereal oils do not occur—indeed I am doubtful if the presence of these is a xerophytic adaptation, although many desert plants possess them. Secretory cavities are found in *Franklandia*, and I have recently seen cavities like oil-glands in a species of *Conospermum*.

The conditions causing xerophytism are many—excessive heat, intense light, small rainfall, drying winds, great cold, hot water, as near volcanic springs, light

or poor soils or those containing salt or other substances injurious to plant life (as vegetable acids derived from humus) are all concerned in bringing about these adaptations.

Some xerophytes, when grown in moist conditions, respond by producing foliage of a mesophytic type, probably a reversion to ancestral form, as in the well-known case of *Ulex Europaeus*. But the Proteaceae have their characters so firmly fixed that they do not alter even under the most favourable circumstances. Alterations do certainly occur, but very rarely. For instance I once found a plant of *Hakea pugioniformis* growing on a sand-dune almost at the edge of the sea, which had the leaves greatly thickened and succulent; but this was merely adding another xerophytic character to those already possessed by the plant.

Mr. L. Rodway, Government Botanist of Tasmania, in a letter informs me that the Tasmanian Proteaceae grow in any soil, wet or dry and in any physical or chemical condition. "*Banksia marginata* grows in any soil, wet or dry, and in any chemical or physical condition. *Hakea lissocarpha*, *H. macrocarpa*, and *H. epiglottis* are almost marsh plants. *H. pugioniformis* will struggle along in dry places but prefers plenty of moisture. *Grevillea australis* grows in wet places at a high altitude. In fact, with the exception of *Persoonia juniperina*, which prefers sandy heaths, the Tasmanian Proteaceae flourish in wet places." Yet in the material which Mr. Rodway sent me I can detect no modification or diminution of the xerophytic characters. Probably the soil conditions and the presence of vegetable acids account for the retention of these characters, but I am inclined to think it is due to heredity—the characters have been so long fixed that no alteration in environment will affect them.

I saw a notable instance in *Banksia integrifolia*, growing in the rich basaltic soil of a gully between Mt. Wilson and Mt. Irvine. In the sandy soil near the coast the tree has cuneate leaves not more than six inches in length, the margin usually entire, but sometimes slightly serrate. The upper surface is smooth and dull green. So far as I have seen the trees in this habitat rarely exceed thirty feet in height. But at Mt. Wilson they are at least seventy feet high. In full grown trees the leaves are similar to those of the coast tree, but in young trees from ten to twelve feet in height they are lanceolate, eighteen inches long, very dark green and shining on the upper side, and have a strongly serrated margin. This is the most remarkable instance of alteration brought by environmental change that I have seen but it was an alteration in external form only—sections of the leaves showed the characteristic structure of the coast plant.

In *Hakea trifurcata* and several other species with terete leaves, the plants bear reversionary leaves in their ordinary habitat. The bulk of the leaves are terete, but the plants have large numbers of flat leaves up to three inches in length, and elliptical to spathulate in shape. This is not due to any change of environment, for in their native habitat the flat leaves are just as numerous as they are under cultivation.

Professor J. B. Cleland some years ago showed me a very peculiar example of alteration in a plant of *Hakea vittata* which he had grown from seed in his garden. The plant at first had terete leaves, but after a time flat leaves appeared, which seems to be the opposite of what one would expect. *Hakea orthorrhyncha* also shows a considerable amount of variation, as will be seen later. But the altered leaves in every case are just as xerophytic in structure as the ordinary leaves and show no approach to the structure of a mesophytic leaf.

Notwithstanding their very perfect adaptation it is very noteworthy that the Proteaceae are very sparsely distributed in the arid and semi-arid regions of Australia, both in regard to species and individuals. For instance, in the Broken Hill district only three of the family have been found, and these in small numbers, while the apparently less efficiently protected Eucalypts, Acacias, Eremophilas and Salt-bushes are numerous both as to species and individuals. The same paucity of Proteads is noticeable all over Central Australia. It is also remarkable that these members of the family which are most highly specialized (such as *Banksia* and *Dryandra*) do not occur in these dry regions. The stronghold of the family is the belt of well-watered country bordering the Continent, and possessing a sandy soil. It therefore seems to be the edaphic factor which governs the distribution of the Proteaceae—they require a highly siliceous soil.*

Mr. E. Cheel has recorded[3] the presence of what may be possibly mycorrhizae on the roots of some of these plants, and if this is correct it is probable that it accounts for their scarcity in the dry interior—the fungi may not be able to grow under these extreme conditions.

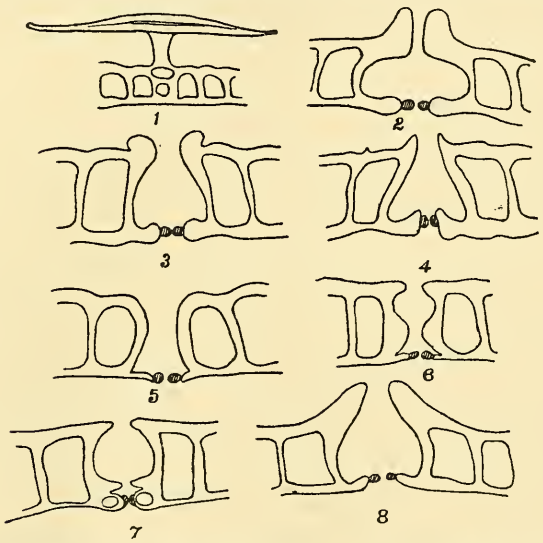
Genus Hakea.

For the purpose of this paper, the Hakeas may be divided into two groups—those with flat and those with terete leaves. Both groups contain species with entire and with divided leaves. As before noted in some species it is common to find both on the same plant. There are a few species which fall between the two main groups; they are flattened but very narrow. These I shall deal with among the terete species.

The flat-leaved species have a vertical orientation, and are all centric. A few, as *H. cucullata* and *H. auriculata*, are not vertical, but the structure is also centric. The leaves are thick (but in varying degree), flat and leathery. The margin may be entire or toothed, and in the latter case the tooth ends in a prickle formed by the vein running through it. A few, as *H. ceratophylla*, have divided leaves. The surface of the leaf is generally dull, but there is no coating of bloom, wax or varnish, even on the young leaves. There are only a few species with a persistent coating of hairs, and that is very sparse, but all are hairy in the juvenile stage. The hairs are T-shaped (Text-fig. 1), the pedicel being very short. They are thick-walled, with a very narrow lumen, and are silvery or ferruginous in colour. The arms drop off early in the life of the plant, but the pedicel persists and later becomes embedded in the epidermis. In a paper on *H. dactyloides*[5] I spoke of these as capitate hairs, but further investigation showed their real nature. Solereder[7] says that these hairs are probably found in every species of *Hakea* and *Grevillea*, and my experience confirms that opinion, as I have found no species of either of these two genera without them. The epidermis is thick, with highly cutinized cuticle, the thickness increasing with age. The thickness of the epidermis varies from 0·02 mm. in *H. undulata* to 0·103 mm. in *H. incrassata*. The cuticle is from 0·003 in *H. undulata* to 0·04 mm. in *H. ceratophylla*. The

* Since this was written, I have read the recent paper by McLuckie and Petrie, "An Ecological Study of the Flora of Mount Wilson, Pt. iv" (These Proceedings, 1927, pp. 161-184) in which the authors state that the main contributing factor in xerophytism is the low water-retaining capacity of light sandy soil, and on consideration, I think that this is probably the case. It must be remembered, however, that in no locality, so far as my experience goes, are Proteads plentiful on non-sandy soil, wet or dry, while on the other hand, they are found in numbers on sandy soils which are always wet and even swampy.

lateral walls of the cells are thin and the cavities are usually empty, but sometimes contain crystals of calcium oxalate, tannin, or in a few cases, a substance staining faintly with picric-anilin blue. The outer surface of the cuticle is often ridged and there is sometimes a ridge-like thickening in the lateral walls of the cells surrounding the orifice of the air-chamber above the guard cells (Plate xxiii, fig. 1). The cells which lie round this cavity (which I shall call the vestibule) in many species project above the general surface of the leaf; there is thus formed a crater-like opening to the stomata. Hypoderm, in the ordinary sense of the word, does not occur, but in a few species a sheet of sclerenchymatous fibres lies just under the epidermis. The vestibule may be bell, dome, funnel, or hourglass shaped (Text-figs. 2-8). In *H. corymbosa* it is hourglass shaped, and Solereder[7] says that in *H. cyclocarpa* it is double-funnel shaped (Text-fig. 5), but in my sections it is cylindrical, somewhat constricted in the middle, but not so much as to be hourglass shaped. In *H. cucullata* I observed a few much constricted in the middle (Text-fig. 7), but the majority were the usual type. The guard-cells are at the bottom of the vestibule on a level with the top of the palisade cells.



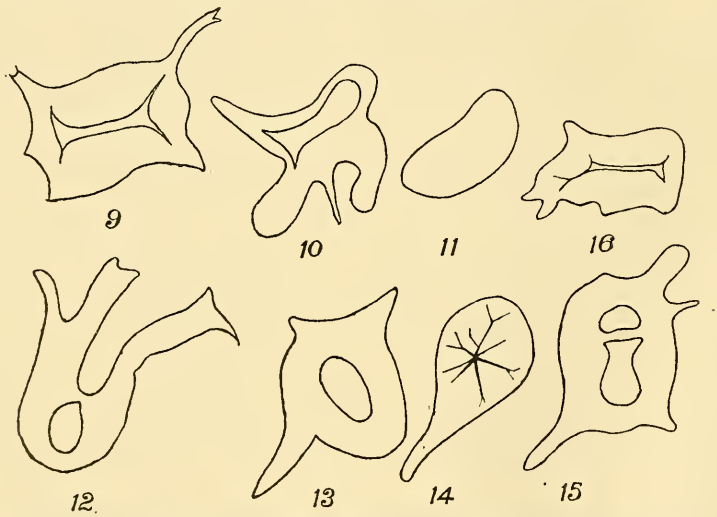
Text-figures 1-8. 1. Two-armed hair. 2-8. Vestibules of stomata. 2, *H. macrocarpa*; 3, *H. Hookeriana*; 4, *H. arborescens*; 5, *H. amplexicaulis*; 6, *H. megalosperma*; 7, *H. cucullata*; 8, *H. linearis* and *H. ruscifolia*. The figures are diagrammatic.

The vascular bundles run through the central region; they are often prominent on the lower or on both sides of the leaf. They vary considerably in number, size, position in the mid-region, and in the amount of sclerenchyma fibres which accompany them. In most species the conducting tissue is in very small proportion to the sclerenchyma fibres which enclose it.

The most characteristic feature of the leaves of the genus is the enormous development of sclerenchyma. It occurs in three forms—fibrous, columnar, and massive. Fibrous sclerenchyma is found in every member of the genus. It usually occurs in connection with the vascular bundles, a strand running along the upper and lower sides of the bundles, and in some cases all round. Sometimes a sheet

of fibres lies just under the palisade, a feature in which they resemble the Banksias. The large amount of sclerenchyma has a very marked stiffening effect on the leaf.

The columnar variety is almost general in the genus, a few exceptions occurring among both flat and terete leaved species, but in some of the flat-leaved forms there are only a very few columns. The columns are cylindrical, spreading out at the top and bottom like the base and pediment of a pillar (Text-fig. 17). In some species the extensions are so wide that they form an almost continuous sheet between the palisade and the epidermis (Text-fig. 19), and sometimes spikes or pegs grow up from this through the lateral walls or even through the cavities of the cells (Text-fig. 19). At the lower end they often send off root-like processes, which penetrate the mid-region and sometimes unite with the outer row of storage cells, thus thickening their walls very considerably. Some of the massive sclereides (when they occur among the palisade cells) appear to be derived from the columns of secondary growth but those in the mid-region are of independent origin. They are of irregular and extraordinary shapes (Text-figs. 9-16). The amount of sclerenchyma in the leaves of the Hakeas is very large—some species as much as 50%, and in *H. multilineata* and *H. obtusa* even more.



Text-figures 9-16. Forms of detached sclereides. 9-13 and 16, *H. corymbosa*; 14 and 15, *H. cucullata*.

There are several distinct types of leaf structure although there is a general resemblance all through the flat-leaved Hakeas. Solereder[7] quotes Jönsson's classification of the leaf structure of the Proteaceae from which the following is an extract.

I. *Hakea*-type. Leaf structure centric; sclerenchyma cells in palisade tissue. Species of *Adenanthos, Grevillea, Hakea, Isopogon, Molloya, Petrophila, Roupala,* and *Stenocarpus.*

II. *Isopogon*-type. Leaf structure centric; ordinary sclerenchyma cells. Species of *Bellendena, Hakea, Isopogon, Leucadendron, Nivenia, Sorocephala* and *Xyloneluni.*

V. *Synaphea*-type. Leaf centric; sclerenchyma of the vascular bundles vertically transcurrent. Species of *Hakea* and *Synaphea.*

There are, however, many other differences among the various species of flat-leaved *Hakea*, and I propose to arrange them according to these peculiarities, as follows:

Group I. Species with thick leaves; palisade in two rows; central region with thick-walled cells; columnar and fibrous sclerenchyma both present (Plate xxiv, fig. 1).

H. macrocarpa A. Cunn. The leaf in this species is thick and smooth. Bentham[1] says "Minutely pubescent on both sides", but I have not been able to detect pubescence in the mature leaves in herbarium specimens In sections, however, the persistent bases of the hairs are seen embedded in the epidermis. The leaf is 0·52 mm. thick, in the thinner places between the veins, and 0·84 mm. at the prominent midrib.

The epidermis is 0·05 mm. and the cuticle 0·03 mm. The lateral walls of the cells are thin and they often contain tannin. There are stomates on both sides, and the epidermal cells surrounding the stomatal opening are slightly raised above the general surface of the leaf. The vestibule is dome shaped (Text-fig. 2) and is 0·06 mm. wide, and the guard cells are at the level of the top of the palisade cells. There are two rows of palisade cells with a total depth of 0·16 mm., and they are closely packed except where they open out in an air-chamber under the guard-cells. The lower row is continuous under the air-chamber. The mid-region is from 0·24 to 0·28 mm. across and is made up of thick-walled cells frequently containing starch and sometimes tannin. Columnar stereides run through the palisade; they are slender and rather sparsely distributed; they spread slightly under the epidermis and send out root-like processes which coalesce with the walls of the outer layer of storage cells beneath, thickening them very much (Text-fig. 17).

Five large veins run through the mid-region, accompanied on both top and bottom by narrow strands of sclerenchyma fibres, the diameter of the whole bundle being 0·4 mm., while the conducting part of the vein is 0·3 mm. On the ventral side the cord of fibres is not so thick as on the dorsal. Besides these five veins there are many smaller ones just beneath the palisade on the ventral side; these have no accompanying strand of sclerenchyma.

H. arborescens R. Br. This has rather a thick leaf, ranging from 0·56 to 0.7 mm. The epidermis is ridged; on the greater part of the leaf it is 0·04 mm. thick, but on the margin it thickens up to 0·07 mm. The cuticle is 0·016 to 0·04 mm. thick, and is highly cutinized. The vestibule is conical (Text-fig. 4) and does not project above the general surface of the leaf; it is 0·03 mm. wide. The palisade is in two rows and has a total depth of 0·16 mm. There is a great development of sclerenchyma. The columnar stereides are 0·02 mm. thick, and spread out slightly at the top; they send out root-like processes at the base but these do not unite with the walls of the storage cells as they do in some other species (Text-fig. 22 and Plate xxiii, fig. 2). The central region is 0·24 to 0·26 mm. wide, and consists of thick-walled cells, many filled with tannin in which starch grains are embedded. The veins are numerous but small, the largest being 0·3 mm. in diameter and the conducting tissue 0·16 mm., but the majority are much smaller than this.

H. cyclocarpa Lindl. Leaf thick, 0·64 mm., epidermis 0·04, and cuticle 0·02 mm. The palisade is in two rows, closely packed and 0·14 mm. deep. The central region is made up of thick-walled cells and is 0·14 mm. across. The veins are small and sub-equal, 0·2 mm. in diameter and the conducting tissue 0·12 mm. There are many columnar sclereides spreading out beneath the epidermis and

above the central region. Throughout the central region there are many bundles of sclerenchyma fibres apart from those capping the veins.

H. Roeii Benth. Leaf thick, 0·74 mm. Epidermis 0·06 mm., and the cuticle 0·04 mm.; vestibule 0·18 × 0·14 mm., with the edges of the orifice projecting above the surface of the leaf. The palisade is two rows 0·16 mm. deep and the cells 0·018 mm. in diameter. The columnar stereides are very numerous, and spread a little at the top and bottom, the outgrowths uniting with walls of the storage cells of the middle region (Text-fig. 22). This last is 0·42 mm. deep and is composed of thick-walled cells, many filled with starch and a few with tannin scattered irregularly about. The vascular bundles are numerous but small, the midrib being very little larger than the others; it is 0·32 mm. in diameter and the conducting tissue 0·14 mm. They all have caps of sclerenchyma on both ends and these extend laterally so that the bundles are almost entirely enclosed. Just beneath the palisade (but separated from it by a single layer of thick-walled cells) there are many bundles of sclerenchyma fibres.

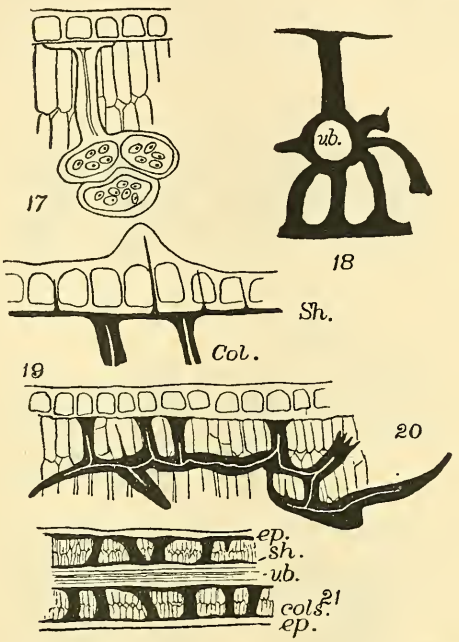
H. Hookeriana Meiss. Leaf thick, 0·72 mm., the epidermis 0·04 mm., and the cuticle 0·02 mm. The vestibule is bell-shaped (Text-fig. 3) and 0·06 × 0·04 mm. There are two rows of palisade cells with a total depth of 0·24 mm. The columns are numerous and spreading at top and bottom. At the base they form irregular masses, penetrating the mesophyll. This last consists of thick-walled cells, but not so thick as in the preceding species; it is 0·3 mm. across. The veins are few and very small, the largest being only 0·06 mm. in diameter and the conducting tissue 0·04 mm.

H. incrassata R. Br. The leaf is 0·74 mm. thick, with a smooth surface. Epidermis 0·05 mm. and cuticle 0·01 mm. thick. Palisade in two rows, 0·14 mm. deep. The medullary tissue is 0·28 mm. across and made up of thick-walled cells, very many filled with starch or tannin. The columnar stereides are very numerous and closely spaced; they often join at the base. Bundles of fibres lie almost continuously under the palisade, but separated from it by a layer of storage cells. The veins are few, their long diameter is 0·36 mm. and the conducting bundle 0·08 mm.

H. flabellifolia Meiss. The leaf of this species resembles that of *H. Brownii* closely both in external form and in internal structure. The veins are, perhaps, a little less in diameter, and the epidermis a little thicker. The leaf is 1·6 mm. thick; the epidermis 0·08 mm. and the cuticle 0·02 mm. The palisade is in two rows, the cells rather slender with a depth of 0·18 mm. The central region is composed of thick-walled cells, many filled with tannin, it is 0·32 mm. across. The veins are rather small, 0·28 mm. in diameter and the conducting tissue 0·14 mm. There are numerous columns but perhaps not so many as in *H. Brownii*, and they do not spread out so much at the top and bottom as in that species.

H. Brownii Meiss. The leaf is very thick, 0·92 to 1 mm., the epidermis 0·06 and the cuticle 0·02 mm. The vestibule is conical and rather wide (Text-fig. 4). The palisade is in two rows and closely packed. It is 0·2 mm. deep. Thick-walled storage cells occupy the midregion which is 0·4 mm. across; many of these cells are filled with tannin. The veins are 0·5 mm. in diameter and the conducting tissue is 0·2 mm. A very large number of stereides traverse the palisade so that at least 50% of that region is composed of sclerenchyma. The tops and bases of these spread out a good deal so that there is a continuous sheet under the epidermis in places. Here and there small masses of sclerenchyma develop in the cavities of the epidermis (Plate xxiii, fig. 4).

H. Baxteri R. Br. The leaf is 0·74 mm. thick, with a smooth surface but the cells round the orifice of the vestibule project above the surface. The epidermis is 0·07 mm. and the cuticle 0·025 mm. thick The vestibule is bell-shaped and is 0·06 × 0·08 mm. The air-chamber beneath the guard cells goes the full depth of the two palisade layers, which have a total depth of 0·12 mm. The middle of the leaf is occupied by thick-walled cells; it is 0·32 mm. wide; many of the cells are



Text-figure 17. Extension of base of column thickening walls of storage cells. 18. Section perpendicular to axis of vein, bases of columns enclosing vascular bundle. 19. Spike-like extensions from sclerenchyma penetrating the epidermis; *H. ruscifolia.* 20. *H. ambigua,* columns sending root-like extensions between the two rows of palisade cells. 21. Section parallel to plane of leaf, *H. amplexicaulis,* column extensions enclosing vascular bundle. The figures are diagrammatic.

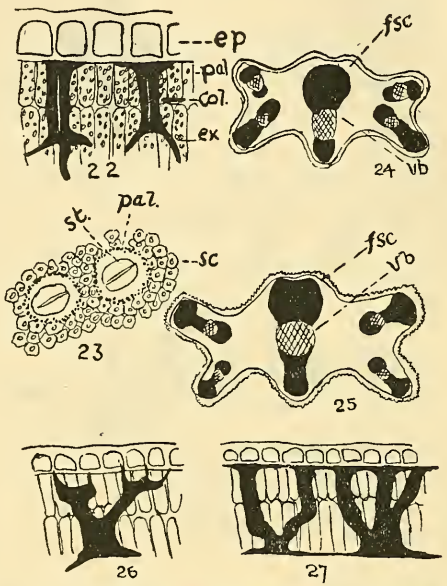
ep. = epidermis, vb. = vascular bundle, col. = columnar stereides, sh. = sheet of sclerenchyma formed by coalescence of tops or bottoms of columnar sclereides.

full of starch or tannin or both. A few thick veins run through this part, 0·4 mm. in long diameter, the conducting tissue being 0·24 mm. The columnar stereides are not numerous; they spread out at the top, forming a sheet under the epidermis; at the base they send down extensions into the mid-region and these frequently coalesce with the storage cells of the outer layer, thickening them very much.

H. ceratophylla R.Br. This species is notable for the extreme range of shape in the leaf, which is divided. It is 0·9 mm. thick, with a slightly ridged surface. The epidermis is 0·06 mm. and the cuticle 0·04 mm. in thickness. The vestibule is conical and slightly depressed below the leaf surface; it is 0·02 mm. × 0·04 mm. The palisade is in two rows, the cells rather slender, and it has a total depth of 0·16 mm. The medullary tissue is 0·5 to 0·54 mm. thick, and consists of thick-

walled cells which are filled with starch, those surrounding the veins are full of tannin (Plate xxiii, fig. 3). The stereides are thick—0·04 mm. They expand at the top, forming a sheet under the epidermis and the lower extremities unite with the upper layer of storage cells. The vascular bundles extend from the upper to the lower epidermis, and are heavily capped with sclerenchyma fibres on both sides.

H. Candolleana Meiss. This species has narrow leaves varying from 1 to 4 mm. in width, but the structure is identical in each. The leaf is 0·44 mm. thick, epidermis 0·07 mm. and the cuticle 0·025 mm. The vestibule is narrow and conical.



Text-fig. 22. *H. amplexicaulis*, root-like extensions of columnar stereides. 23. *H. pandanicarpa*, section parallel to plane of leaf showing arrangement of palisade, and sclerenchyma round the stomates. 24. *H. pycnoneura*, sectional outline of leaf showing arrangement of veins and bundles of sclerenchyma fibres. 25. *H. Morrisonianum*, section of leaf, showing arrangement of veins and bundles of sclerenchyma fibres. 26 and 27. *H. ambigua*, branching columns. (All diagrammatic.)

col. = columnar stereides, ep. = epidermis, ex. = root-like extensions, fsc. = fibrous sclerenchyma, pal. = palisade, sc. = sclerenchyma fibres, st. = stomate, vb. = vascular bundle.

There are two rows of palisade, 0·14 mm. deep. The central region is made up of thick-walled cells containing much starch, and very many tannin filled, it is 0·6 mm. across. The mid-vein is 0·24 mm. in diameter, and the conducting tissue 0·14 mm. Unlike most of the other species the sclerenchyma caps do not encroach on the palisade. The minor and marginal veins are just beneath the palisade, but the mid-rib is midway between the upper and lower layers. The marginal vein has a thick strand of sclerenchyma fibres below, and a little to one side. There are many slender columns which have extended bases but do not spread at all at the top. More than twenty bundles of sclerenchyma are found beneath the palisade tissue.

H. falcata R.Br. The leaf is from 0·6 to 0·65 mm. thick with a ridged epidermis, the latter 0·08 mm., and a rather thin cuticle, 0·02 mm. The vestibule is dome-shaped 0·05 mm. wide; the surrounding epidermal walls do not project above the leaf surface. The palisade is very closely packed and is 0·14 mm. deep. The central region is 0·2 to 0·25 mm. across; some of the cells are pitted. The middle vein is 0·5 mm. and the conducting tissue 0·3 mm. There are not many columns.

H. pycnoneura Meiss. This species and the next resemble *H. florida* and *H. falcata* in the hardness of their leaves but they are also remarkable for their sectional outline (Text-figs. 24 and 25). Their leaves resemble those of some of the Grevilleas, and so far as my experience goes, they stand alone amongst the Hakeas. The leaf of this species is 0·66 mm. thick, and carries a great many two-armed hairs, the arms of which drop off while the bases persist and become embedded in the epidermis. The epidermis is very deeply ridged and the cavities of the cells large; it is 0·06 mm. thick and the cuticle 0·02 mm. The palisade cells are very tightly packed and only 0·1 mm. deep. The central region is 0·32 mm. wide, the cells are very thick-walled, a few contain tannin. There is a large central vein with a heavy capping of sclerenchyma on the dorsal side. This and the next species differ from the majority of Hakeas in having no columnar sclereides.

H. Morrisonianum. The central flat part of the leaf is 0·4 mm. thick, while the dorsal and ventral lobes on each side are 0·48 mm. and 0·44 mm. respectively. The epidermis is 0·08 mm. thick, thinner on the lobes, and thickly covered with T-shaped hairs in the juvenile stage. The vestibule is narrow-conical, 0·02 mm. wide and projects above the surface. The central region is 0·16 to 0·24 mm. wide, and made up of very thick-walled cells. The palisade is not deep—0·1 mm.—and is very closely packed. The veins extend from the floor of the upper epidermis to that of the lower, and are very heavily capped with sclerenchyma fibres, the conducting tissue being barely 0·1 mm. As in the last species, there is a central vein and one in each lobe.

H. florida R.Br. Leaf 0·34 mm., epidermis 0·04 mm., cuticle smooth, 0·016 mm., vestibule not projecting, broadly bell-shaped, 0·04 mm. wide. Palisade in single row 0·1 mm. deep. Cells of central region not as thick as in most other species, 0·1 mm. in diameter. Middle vein 0·5 mm. across and the conducting tissue 0·3 mm.; the marginal and smaller veins being lightly capped with sclerenchyma.

H. pandanicarpa R.Br. This is a very remarkable species, having an arrangement of the palisade and stereides that I have found in only one other species. The leaf is thick—0·92 to 0·96 mm.; the epidermis 0·03 mm. and the cuticle 0·02 mm. The orifice of the narrow bell-shaped vestibule does not project above the leaf surface. The palisade is in two rows, 0·24 mm. deep. The medullary tissue is 0·32 mm. across and consists of thick-walled cells, many containing starch, and a few near the middle filled with tannin (Plate xxv, fig. 3). There are a great many stereides, rather slender, 0·02 mm., spreading a little at the top, and much more at the base, with root-like extensions which often penetrate the mid-region. The storage cells of the outer layer have their walls much thickened by union with these. The veins are few and small, they are capped with bundles of sclerenchyma on both sides.

The remarkable feature of the leaf is the arrangement of the sclereides and palisade in relation to the stomates. Under each stomate there is a cylindrical cavity or air-chamber, surrounded by one row of palisade cells; outside this there

is a circle of columnar stereides two or three rows deep, the tops and bottoms extending so as to touch each other, while the slender shafts leave openings for the free interchange of gases (Text-fig. 23). This is the most elaborate provision against excessive transpiration that I have seen in the Hakeas (Text-fig. 23 and Plate xxiv, fig. 2). It occurs only in this species and in *H. clavata*.

H. clavata, Labill. This species does not fit into any of the groups in which I have arranged the Hakeas, but I have placed it here on account of the arrangement of the stomates, palisade, etc., this being similar to that of *H. pandanicarpa* (Plate xxiv, fig. 2). There is, in the herbarium of the Sydney Botanic Gardens, an undetermined species collected by the late Mr. J. H. Maiden at Esperance, W.A., which has the same structure, but as it has no point of difference except a much shorter leaf, I have no doubt but that it is the same species.

The plant has very thick leaves closely resembling those of *Petrophila linearis*; they are 3·2 mm. thick, epidermis 0·04 mm. and cuticle 0·02 mm., vestibule bell-shaped, 0·06 mm. wide, palisade in two rows 0·32 mm. wide. The central region is 2·48 mm. across and is composed of very thin-walled cells (Plate xxiv, fig. 3). It is difficult to say that there is any chlorophyll in them; only herbarium material was available. At the base of the palisade cells some of the central cells stained a faint blue which might indicate chlorophyll. These thin-walled cells are much larger than the thick-walled cells of this group, ranging from 0·06 to 0·15 mm. in diameter. Bentham describes the leaf as veinless, but there are a few veins, very small and narrow, and with very little xylem. They are distributed just under the palisade, and one is in the centre. There is no sclerenchyma anywhere in the mid-region.

H. obtusa Meiss. Bentham[1] says: "The young shoots silky-tomentose, the adult foliage glabrous". But in the specimens seen by me, the old leaves were slightly hairy. This species might almost be placed in a section by itself, as the mesophyll is composed of very thick-walled cells unlike those of any other species (Plate xxv, fig. 2). This makes it extremely hard, and very difficult to section without breaking up.

The leaf is 0·6 mm. thick, the epidermis 0·06 mm., and the cuticle rather thick —0·04 mm. The palisade is in two rows, 0·14 mm. deep. The thick-walled cells of the mesophyll are rather longer than broad, the long axis being perpendicular to the plane of the leaf; the small cavities being sometimes filled with tannin and sometimes with a substance staining faintly with picric-anilin blue; this region is 0·28 mm. across. The main vein is 0·6 mm. in diameter and the conducting tissue 0·06 mm. The marginal vein is heavily capped with sclerenchyma. There are very few columnar sclereides, and those there are seem to arise from the sclerenchyma of the central region and grow outwards towards the epidermis through the palisade layer.

Group II. Leaves rather thinner than in the previous group; palisade in one row (except in *H. marginata*); cells of mid-region elongated or rounded, and containing chlorophyll (Plate xxv, fig. 4.)

H. megalosperma Meiss. The leaf is rather thick, 0·5 mm., the epidermis 0·05 mm., ridged, cuticle 0·02 mm. The vestibule opens widely and is constricted in the middle (Text-fig. 6). The palisade is in two rows and is 0·12 mm. deep. The veins are small and sub-equal, 0·22 mm. in diameter, with conducting tissue 0·12 mm. There are many columns and they spread widely at the base and apex; where they are over a vein they almost enclose it.

H. amplexicaulis R. Br. Leaf 0·4 mm. thick; epidermis 0·04 mm., smooth, the lateral walls ridged like those shown in Plate xxiii, fig. 1; cuticle 0·02 mm.; vestibule a narrow reversed funnel, and depressed (Text-fig. 5). Palisade in one row 0·1 mm. deep; central region 0·12 mm. across, made up of thin-walled cells containing chlorophyll. There is a midrib 0·68 mm. in diameter, the conducting tissue being 0·5 mm., and a number of smaller veins. The columns are numerous and spreading at the top and much more at the bottom. Over the veins the extensions come into contact with each other and form a sheath to the vein (Text-figs. 18 and 21).

H. glabella R. Br. The leaf is 0·4 to 0·5 mm. thick, the epidermis is 0·04 mm., and the cuticle 0·02 mm.; the vestibule is shallow and cylindrical, and the surrounding cells project above the leaf surface. The palisade is in one row and is 0·1 mm. deep; the central region is 0·12 mm. across. The columns of sclerenchyma are few and spread at the top but not at the base. There is one main vein, 0·56 mm., lightly capped with fibres, and a number of smaller ones, each of which has a bundle sheath, a feature not common in Hakeas.

H. cristata R. Br. The leaf is 0·52 mm., slightly ridged, epidermis 0·06 mm., and cuticle 0·02 mm. The palisade is in one row 0·16 mm. deep; the central region 0·1 mm. across. The stereides spread at both ends and form a partial sheath to the vascular bundles.

H. linearis R. Br. The leaf is rather thin, 0·38 mm., epidermis 0·06 mm., and cuticle 0·02 mm.; the vestibule projects so as to form a cone round the orifice, as also in *H. ruscifolia* (Text-fig. 8). The palisade is in one row and 0·1 mm. deep; the central region is 0·12 mm. across. The columnar stereides spread out at the upper and lower extremities and form a sheath to the vascular bundles as in the last two species. The main vein is 0·32 mm. in diameter and the conducting vessels take up 0·24 mm. of this. The marginal veins are small and have a cap of fibres on the ventral, but none on the dorsal side; a good many tannin cells are near the veins.

H. ferruginea Sweet. Leaf thin, 0·26 mm., epidermis 0·04 mm., and cuticle 0·01 mm.; vestibule conical, 0·04 mm. wide; the palisade is in one row 0·08 mm. deep. The central region 0·1 mm. across. A rather unusual feature is the complete absence of columnar stereides, and there is very little fibrous sclerenchyma.

H. marginata R. Br. The leaf is of medium thickness, 0·42 mm., the epidermis 0·04, and the cuticle 0·01 mm. The vestibule is bell-shaped and does not project above the leaf surface. The palisade cells are in two rows with a total depth of 0·08 mm., and are very closely packed. The central region is 0·2 mm., and consists of thin-walled chlorenchymatous cells closely packed. The main vein is 0·4 mm. in diameter and is completely surrounded by sclerenchymatous fibres, the conducting vessels taking up 0·2 mm. of this. There is a strong marginal vein, also surrounded by sclerenchyma. The other veins are small and heavily capped with fibres on both faces. There are many columns in the palisade, and some irregular massive ones in the central region, some of the arms of which penetrate the palisade and take the form of columns.

Group III. Leaves thick or rather thin; palisade in two rows; medullary region occupied by chlorenchymatous cells arranged in an open network like the spongy tissue in mesophytic leaves (Plate xxiv, fig. 4).

H. auriculata Meiss. The leaf is 0·36 mm. thick (at the midrib it is 0·86 mm.), epidermis 0·04 mm., and cuticle 0·02 mm. Vestibule bell-shaped and depressed, 0·04 mm. wide. Palisade in two rows 0·16 mm. deep; central region 0·1 mm.

across. Midrib 0·68 mm. in diameter, the conducting tissue being 0·34 mm. The small marginal vein has no capping.

H. eriantha R. Br. The leaf is 0·4 mm. thick, epidermis 0·04 mm., cuticle 0·02 mm. Palisade in two rows 0·18 mm. deep. Central region 0·08 mm. across. The main vein is 0·38 mm. in diameter and the conducting tissue 0·16 mm. The columns are numerous and spread at the top and bottom; near the veins the bases enclose them.

The outstanding feature is the narrowness of the mid-region; the palisade and columns of each side almost meet at their bases.

H. lasiantha R. Br. The leaf is 0·44 mm. thick, epidermis 0·03 mm. The cuticle is very thin, 0·005 mm. The palisade is two-rowed, 0·1 mm. deep. The spongy chlorenchyma is 0·1 mm. across. The main vein is 0·54 mm. across, with a conducting tissue 0·3 mm. There are numerous columns, irregular in shape, and spreading both at top and bottom; sometimes the inner extensions entirely enclose a vein, especially the marginal vein.

H. ruscifolia Labill. Leaf 0·4 mm. thick, epidermis 0·04 mm., and cuticle 0·02 mm.; the walls of the vestibule are raised so as to form a conical projection above the surface of the leaf, rather higher on the ventral side than on the dorsal, the cavity being 0·02 mm. wide (Text-fig. 8). Palisade in one row, 0·1 mm. on the ventral side and 0·06 mm. on the dorsal. Medullary tissue a very open network 0·04 mm. wide. The central vein 0·16 mm. in diameter and the conducting vessels 0·08 mm. The smaller veins are narrowly capped as is the marginal vein.

The columnar sclereides are numerous, many of them curved; they all spread out at the apex and base. At the apex they form a continuous sheet under the epidermis, and from this sheet pegs or spikes grow up through the lateral walls of the epidermal cells and sometimes through the cavities (Text-fig. 19). At the base the columns also spread out, and where they are over a vein they coalesce to form a sheath enclosing it completely (Text-figs. 18 and 21).

H. saligna R. Br. Leaf 0·48 mm. thick, epidermis 0·03 mm., cuticle 0·01 mm.; vestibule conical, 0·02 mm. wide, and projecting very slightly above the surface of the leaf; palisade in one row 0·1 mm. deep; central region 0·2 mm. across, and made up of a rather closely packed network of cells, many, especially near the veins, being filled with tannin. Veins sub-equal, 0·36 mm. in diameter, the conducting tissue being 0·16 mm. De Bary, quoted by Solereder, mentions "the occurrence of solitary crystals in the epidermis", but I have never seen any in the sections I have examined, but I find that the occurrence of crystals is often sporadic, one leaf showing numbers while another from the same plant has none.

H. multilineata Meiss. Leaf 0·38 to 0·4 mm., epidermis 0·08, and cuticle 0·04 mm. thick; vestibule bell-shaped, 0·03 mm. wide; palisade in one row, varying in depth 0·2 mm. at most. Medullary region 0·16 mm. wide, the cells small and very full of chlorophyll. The veins are sub-equal; the conducting tissue is only 0·2 mm. wide, while the bundles of sclerenchyma run out to the epidermis on each side with a total depth of 0·74 mm. The columns of sclerenchyma are numerous and very massive and irregular. Cannon[2] says, "The sclerenchyma appears to be mainly or wholly fibrous", but in all the sections I have examined there are many columnar stereides. At the margin there is a fan-shaped strand of fibres enclosing a small vascular bundle. The characteristic feature of the leaf is the great quantity of mechanical tissue, at least 50% of the leaf substance being sclerenchyma. This makes it extremely difficult to cut sections. Probably the habitat of the plant—the arid regions—accounts for this.

H. laurina R. Br. This species, though growing in the semi-arid parts of Western Australia, is more mesophytic than any other I have seen, the greater part of the leaf being chlorenchyma. It is 0·36 mm. thick, the epidermis 0·04 mm., and the cuticle 0·01 mm. Vestibule, wide bell-shaped, 0·02 mm. wide. The palisade is in one row, 0·1 mm. deep; mid-region 0·1 mm. across, and made up of a rather close network of cells. One central vein 0·44 mm. across and the conducting tissue 0·12 mm.; the fibres of sclerenchyma almost surround the vein but between the edges there are a few thick-walled cells containing starch; the other veins are all small and have very little sclerenchyma, but the marginal bundle is entirely surrounded by sclerenchyma, the vessel bundle being 0·06 mm. in diameter. There are no columnar sclereides.

H. cucalyptoides Meiss. This variety has rather thinner leaves than *H. laurina*, and the midrib projects on both sides of the leaf considerably more. But in other respects it is quite similar.

According to Haberlandt,[4] Hintz observed water-storage tissue in the leaf margin of various *Acacia*, *Quercus*, *Ilex*, and *Hakea eucalyptoides*. The opinion is expressed that "The margin, which is the region most exposed to damage by excessive loss of water, is provided with a local water tissue composed of a varying number of layers, although water-storage arrangements are altogether absent, or, at any rate, conspicuously less, in the rest of the leaf".

The cells referred to are cells between the sclerenchyma cap of the marginal vein and the epidermis, and they are found at every vein in most species. They are also found under the epidermis wherever the columns spread out to form a sheet at the apex. Haberlandt, however, elsewhere, refers to thick-walled cells as starch-storing tissue. As I have already said, these thick-walled cells may contain starch, tannin, and crystals, and it is quite probable that they may also function as water-storing tissue. But they differ much from the typical water-storing thin-walled cells.

H. corymbosa R. Br. The leaf is 0·32 mm. thick, epidermis 0·04 mm., and cuticle 0·02 mm.; the vestibule is dome-shaped and 0·06 mm. wide. The palisade is in one row, 0·08 mm. deep on the ventral side and 0·06 mm. on the dorsal. Medullary region a very close network, 0·1 mm. across. The middle vein is 0·5 mm. in diameter, and the conducting tissue 0·2 mm.; the caps of fibres extend to the epidermis on each side, but separated from it by a single row of thick-walled cells; the gap between the upper and lower bundles is filled by thick-walled cells containing starch. There are two smaller veins similar in arrangement to the midrib; the marginal vein is capped with fibres on the outside only. The peculiar feature of this species is that there are no columnar stereides, their place being taken by massive sclereides of extraordinary form in both palisade and medullary region (Text-figs. 9-13 and 16).

H. undulata R.Br. Leaf 0·34 mm. thick, epidermis 0·03 mm., cuticle 0·01 mm. Palisade in one row 0·08 mm. deep. Central region a rather loose network 0·16 mm. across. Middle vein 0·44 mm. and conducting tissue 0·16 mm.; there are besides a number of sub-equal veins all lightly capped with fibres; there are no columns but many irregular stereides in the medullary region some of which penetrate the palisade.

H. petiolaris Meiss. Leaf 0·36 mm. thick, epidermis strongly ridged, 0·06 mm., cuticle very thick, 0·04 mm., vestibule bell-shaped, the surrounding cells rising above the leaf surface, 0·06 mm. wide. Palisade in one row, 0·08 mm. on the ventral and 0·06 mm. on the dorsal side. Central region 0·14 mm. across. The

main vein is 0·76 mm. in diameter, and the conducting bundle 0·36 mm., the fibres completely surround the vessels. There are no columns or detached sclereides.

H. neurophylla Meiss. Leaf 0·32 mm. thick; epidermis ridged, 0·04 mm., cuticle 0·015 mm., the surrounding cells projecting above the leaf surface. Palisade one row 0·1 mm. deep. Medullary region 0·12 mm. wide, the cells closely packed. Principal vein 0·46 mm. the conducting vessels being 0·18 mm. There are no columnar or detached sclereides.

H. cucullata R.Br. In this species the leaves are wide, rounded, concave and arranged horizontally on the stem, but the structure is centric. Leaf 0·56 mm. thick, epidermis 0·08 mm. and cuticle 0·04 mm. In specimens from the Melbourne Botanic Gardens the surface is ridged, but in those from the Sydney Gardens it is quite smooth. The vestibule is bell-shaped but in a few instances it is constricted in the middle (Text-figs. 6-7) much as in *Dasylirion filifolius*, figured by Haberlandt.[4] The palisade is one-rowed and is 0·08 mm. deep. The central region is 0·2 mm., the cells very full of starch. Main vein 0·48 mm., and conducting tissue 0·12 mm. The cap of fibres extends to the epidermis on each side, and is only separated from it by a layer of thick-walled cells; on each side of the conducting bundle and between the ends of the bundles of fibres there are about twenty thick-walled cells full of starch. The specimens from Melbourne Gardens have many irregular columnar sclereides sometimes penetrating deeply into the medullary region, especially where the section passed through an injury to the leaf. The specimens from the Sydney Gardens have no columns, but in the central region there are occasional detached sclereides.

H. conchifolia and *H. Victoriae.* These are generally considered to be varieties of *H. cucullata*; the structure is exactly similar.

H. ambigua Meiss. (Plate xxiii, fig. 2). The leaf is 0·56 mm. thick, epidermis 0·06 mm., ridged, cuticle 0·04 mm., vestibule bell-shaped. Palisade in two rows, 0·14 mm. on the ventral and 0·12 mm. on the dorsal side. Central region 0·12 mm. across, the network rather close. The principal vein is 0·5 mm. across and the conducting tissue 0·14 mm.; the whole bundle, as in *H. petiolaris*, is entirely enclosed by sclerenchyma. The columns are few, they branch in an extraordinary manner, sending out horizontal arms between the two rows of palisade and from these upright processes grow between the cells of the palisade like candelabra (Text-figs. 26 and 27).

H. plurinervia F.v.M. Leaf 0·32 mm., epidermis 0·02 mm. and cuticle 0·01 mm. Palisade in one row 0·06 mm. deep. Central region 0·06 mm. Vein 0·38 mm., the conducting tissue being 0·16 mm. There are no columnar or detached sclereides.

H. dactyloides Cav. I have described this species in These Proceedings,[5] and there is nothing to add except to correct the mistake I made in calling the persistent bases of the two-armed hairs capitate hairs. A noteworthy point is the extraordinary massive sclereides, figured in the paper.

H. oleifolia R.Br. Leaf 0·34 mm. thick, epidermis 0·04 mm. and cuticle 0·01 mm., vestibule wide, bell-shaped, 0·06 mm. wide. Palisade one row, 0·06 mm. deep. Central region 1 mm. across. Vein 0·36 mm. in diameter, conducting tissue 0·24 mm. This species is chiefly remarkable for the absence of columns and the very small strands of sclerenchyma. It is, like *H. laurina*, very mesophytic in type.

H. stenocarpa R.Br. Leaf 0·38 mm. thick; epidermis 0·06 mm., cuticle 0·03 mm. Palisade in one row, 0·01 mm. deep; central region 0·1 mm. across. The chief feature is the great development of fibrous sclerenchyma round the midrib. It

is 0·84 mm. vertically and extends 1·3 mm. horizontally, the conducting tissue being 0·28 mm. There are no columnar stereides.

H. varia R.Br. The leaf is 0·54 mm. thick; epidermis 0·06 mm., cuticle 0·02 mm., the vestibule narrow bell-shaped with the cells surrounding the orifice projecting to a height of 0·06 mm. above the surface of the leaf. Palisade in one row, 0·12 mm. deep. Medullary region 0·1 mm. across. Centre vein 0·42 mm. in diameter, the conducting tissue being 0·22 mm. There are many columns which spread out at the apex and base so as to form sheets under the epidermis and above the central region.

The variety *H. intermedia* is identical in structure with *H. varia.*

H. nitida R.Br. Leaf 0·54 mm., epidermis 0·06 mm., cuticle 0·02 mm., vestibule cylindrical but slightly constricted in the middle so as to resemble a dice box, 0·03 mm. wide. Medullary region 0·1 mm. across. The veins are 0·36 mm. in diameter, the conducting tissue being 0·28 mm. The columnar stereides are slender and irregular, the bases extending into the central region.

I have examined an undescribed species in the Sydney National Herbarium, collected by the late J. H. Maiden at Esperance, W.A. It has the ordinary type of structure, the leaf measurements being: Leaf 0·5 mm., epidermis 0·04 mm., cuticle 0·02 mm., palisade one row, 0·18 mm., medullary region 0·12 mm., rather loosely packed, veins 0·35 mm., and conducting tissue 0·14 mm. The columnar stereides are slender and not spreading at the base or apex.

I have not been able to procure specimens of the following species:— *H. stenophylla, H. trineura, H. stenocarpoides, H. cinerea, H. loranthifolia, H. smilacifolia* and *H. carina.* There are also a few more recently described species which I have not seen.

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Literature.

Solereder gives a comprehensive bibliography (although he omits the Australian papers on the subject), but many are theses or dissertations, and no copies could be traced in the Sydney libraries.

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EXPLANATION OF PLATES.

Plate xxiii.

1. Vestibule of stomate showing thickenings in wall of orifice.
2. Root-like extensions of columns in *H. ambigua.*
3. Veins surrounded by cells containing tannin, *H. ceratophylla.*
4. Sclerenchyma spreading into epidermis, *H. Brownii.*

Plate xxiv.

1. Thick-walled cells occupying the mesophyll, *H. Brownii.*
2. Section parallel to plane of leaf showing arrangement of palisade and sclereides round cavity beneath stomate, *H. pandanicarpa.*
3. Thin-walled cells of mesophyll, *H. clavata.*
4. Spongy tissue occupying the mesophyll, *H. undulata.*

Plate xxv.

1. Columnar stereides spreading at apex and base, *H. Brownii.*
2. Mesophyll occupied by very thick-walled cells, *H. obtusa.*
3. Tannin cells running through centre of mesophyll, *H. pandanicarpa.*
4. Mesophyll occupied by elongated cells containing chlorophyll, *H. amplexicaulis.*